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Revision of the genus *Lepidopria* Kieffer (Hymenoptera, Diapriidae, Diapriinae) of the world fauna

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Abstract

All known species of the diapriid genus *Lepidopria* Kieffer, 1911 are revised, keyed and illustrated. A new species, *L. bicarinata* Chemyreva & Ku, **sp. nov.** is described from South Korea. The diagnosis of the genus *Lepidopria*, as well as that of all described species, has been clarified. New data on the distribution of the species *L. masneri* Notton, 1994 and *L. pedestris* Kieffer, 1911 are provided. The association of *L. masneri* with the nests of *Solenopsis japonica* Wheeler, 1928 is reported and the biology of *Lepidopria* species is discussed. Taxonomic status of the mysterious *L. aberrans* Brues, 1916 is considered and a new combination, *Bruesopria aberrans* (Brues), **comb. nov.**, suggested.

Keywords

Bruesopria, Diapriini, myrmecophilic wasps, new records, new species, symphiles, *Solenopsis*, taxonomy

Introduction

Lepidopria Kieffer, 1911 comprises a few species of tiny wasps belonging to the myrmecophilic diapriids (Huggert and Masner 1983). The genus currently includes the following four species: *L. aberrans* Brues, 1916, recorded in Maryland, USA; *L. lloydi* (Ferrière, 1935), recorded in Tanzania; *L. masneri* Notton, 1994, recorded in Japan

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and South Korea; and *L. pedestris* Kieffer, 1911, recorded in Europe. According to Masner and Muesebeck (1968), the *L. aberrans* is doubtfully placed in this genus and may belong to the Nearctic genus *Bruesopria* Wing, 1951 (Huggert and Masner 1983; Masner and García 2002); however, the reasons for the doubts and the morphological features of this species were not discussed. The specific characters of the *Lepidopria* species, such as reduced eye size and number of palpal segments, reduced pigmentation (especially in the female antenna, which has a yellow clava), the secondary apterism, abundant setation, and an enlarged petiole (similar to many ants), suggest that they all have myrmecophilic habits (Notton 1994). *Lepidopria aberrans* and *L. pedestris* were reared from the puparia of tachinid flies, which were found inside adult scarabaeid beetles (Brues 1916; Huggert and Masner 1983). It has also been confirmed that both species are symphilic in the nests of ants of the genus *Solenopsis* Westwood, 1840 (Brues 1916; Ferrière 1927; Hölldobler 1928; Wing 1951; Lachaud 1981b; Lachaud and Passera 1982; Masner and García 2002). The interaction with ants has been studied in detail for only one species, *L. pedestris* (Hölldobler 1928; Lachaud 1980, 1981a, b, c, 1982; Lachaud and Passera 1982).

According these studies *L. pedestris* is a highly adapted myrmecophilous diapriid wasp that lives in close association with the ant *Solenopsis fugax* (Latreille, 1798). The wasp integrates into ant colonies primarily by mimicking or sharing tactile solicitation signals and by producing cuticular secretions that induce intense grooming or licking from ant workers. Adults (especially females) obtain food by trophallaxis from ants inside nests without aggression (Lachaud 1982). Morphological specializations like clusters of active secretory cells opening into dense tufts of hairs on the petiole and anterior part of S2 (these secretions are associated with the regions ants lick most intensively) underlie chemical integration of *L. pedestris* in the ant colony (Lachaud 1981a). The fore leg tapping patterns and antennal contacts are similar to those used by ants and underlie the behavioral integration of *L. pedestris* (Lachaud 1981c, 1982). The success of the wasp's integration is most clearly demonstrated by the fact that workers of *S. fugax* may regurgitate food to newly introduced *L. pedestris* within ~10 minutes and show very little aggression (Lachaud 1981b).

A detailed phenological study of *L. pedestris* was carried out by Lachaud and Passera (1982). Although the authors of this study were unable to establish the primary host of this species, they reached several significant conclusions. Firstly, *L. pedestris* is undoubtedly myrmecophilic; it uses *Solenopsis fugax* nests for protection, feeding purposes and hibernation in winter. Secondly, *L. pedestris* does not use *S. fugax* as a host and does not reproduce in its nest. Thirdly, *L. pedestris* specimens spend most of their life cycle outside the nest (from early spring to late autumn), where they mate, parasitize the primary host and develop into adults, and then, when winter arrives, they return to the *S. fugax* nests. Finally, *L. pedestris* is strictly associated with *S. fugax* nests, since it is not found in the nests of other ant species parasitized by the lestobiotic *S. fugax* and was even eliminated by two of these species (*Plagiolepis pygmaea* (Latreille, 1798) and *Tetramorium semilaeve* André, 1883) when experimentally introduced in their nest (Lachaud and Passera 1982). Only later the main host of *L. pedestris* was re-

ported as tachinid flies, which parasitise scarabaeid beetles that are not associated with ant nests (Huggert and Masner 1983).

Unfortunately, we do not know much about the life histories of other *Lepidopria* species. The African species *Lepidopria lloydi* was reared from puparia of the *Glossina* Wiedemann, 1830 (Ferrière 1935; Notton 2014), whereas the biology of *L. masneri* remains unknown (Notton 1994). These two species have morphology that suggest myrmecophily, however, their connection with ants has not yet been documented.

This work aims to review the morphology and biology of all described species of the genus *Lepidopria*, clarify the diagnostic characteristics of this genus and some closely related genera, and describe a new species of *Lepidopria* from the south-eastern Palaearctic region.

Material and methods

Material observed in this study originates from the several collections: **MCSN** – the Museo Civico di Storia Naturale "Giacomo Doria", Genoa, Italy; **NHML** – the Natural History Museum, London, UK; **NIBR** – the National Institute of Biological Resources, Incheon, Republic of Korea; **SMNE** – the Science Museum of Natural Enemies, Geochang, Republic of Korea; **NMNH** – the National Museum of Natural History, Smithsonian Institution, Washington, USA; **ZISP** – the Zoological Institute of the Russian Academy of Sciences, St Petersburg, Russia; **UATC** – Ulsan Agricultural Technology Center, Republic of Korea.

Most of images were taken with a Nikon stereo microscope SMZ25 equipped with objective lens Plan Apo 1.6× and digital camera DS-10. Some images were taken with a camera Olympus E-M5 Mark II and objective lens M.Zuiko 60 mm 1:2.8 combined with a Raynox MSN-505 (Fig. 7A, C). Final images were stacked using Helicon Focus 7.6.

The morphological terminology, abbreviations and measurements follow Masner and García (2002), Yoder (2004) and the Hymenoptera Anatomy Ontology (Yoder et al. 2010). New regional and country records are indicated with an asterisk (*).

Taxonomy

Genus *Bruesopria* Wing, 1951

Note. A detailed diagnosis of this genus has been given by Masner and García (2002). Therefore, here we give only a short comparative diagnosis of this genus, emphasizing the diagnostic differences between it and the genus *Lepidopria*.

Comparative diagnosis. Female antenna 11–12-merous [only 12-merous in *Lepidopria*], with abrupt 3-merous clava [nonabrupt or 4-merous clava in *Lepidopria*]; posterior margin of propodeum with deep semicircular excavation, median carina of propodeum rudimentary, posterolateral corner of propodeum angular and strongly

projecting [same in *Lepidopria* to with median carina, without excavation of posterior margin and without posterolateral projection]; petiole strongly modified, remarkably higher than long in lateral view, with finger-like projection produced dorsally above anterior margin of T2 (Fig. 1C, D) [same in *Lepidopria* (Fig. 9E) to as long as high in lateral view and not produce dorsally above T2 (Fig. 2C, D)]; base of S2 bare, smooth, flat: not convex medially and not grooved laterally, with deep semicircular excavation of anterior margin (Fig. 1A) [densely setose, with lateral grooves and convex medially, excavation of anterior margin not deep in *Lepidopria* (Fig. 1B)].

Remarks. This genus comprises only two described species from the New World (Wing 1951; Johnson 1992). Masner and García (2002) reported an undescribed species associated with *Solenopsis* sp. in Arizona. An undetermined species of *Bruesopria* (possibly *B. aberrans*) was found by Dr Alexander L. Wild in a colony of *Solenopsis molesta* (Say, 1836) at Konza Prairie in Kansas, USA (see Fig. 1E, F). The biodiversity and morphological variability of the three closely related genera – *Lepidopria*, *Bruesopria*, and *Solenopsia* Wasmann, 1899 – have not yet been sufficiently studied and future discoveries may necessitate the synonymisation of these genera (Masner and García 2002). However, the diagnostic differences between *Lepidopria* and *Bruesopria*, as described above, are presently clear enough to maintain these taxa as valid. Furthermore, these genera have different distributions: all *Lepidopria* species are found in the Palaearctic region, whereas all *Bruesopria* species are found in the Nearctic region.

***Bruesopria aberrans* (Brues, 1916), comb. nov.**
Fig. 1C, D

Lepidopria aberrans Brues, 1916: 126.
Lepidopria aberrans: Masner and Muesebeck 1968: 10.
?*Bruesopria aberrans*: Masner and García 2002: 73.

Material examined. ***Holotype***, • female: USNM no.20474, Hagerstown, Md., [Washington, Maryland, USA] Aug. 15, 1913, ex puparium of ?*Cryptomeigenia theutis* (Walker) in an adult of *Phyllophaga inversa* (Horn); stored in NMNH.

The female of *B. aberrans* can easily be distinguished from other described *Bruesopria* species by its 12-merous antennae, whereas males of all known *Bruesopria* species have not been described or illustrated in detail (Wing 1951). Some details about *Bruesopria* male morphology are known only from the diagnosis of this genus given by Masner and García (2002).

Biology. *Bruesopria aberrans* was reared from the puparium of a tachinid fly (possibly *Cryptomeigenia theutis* (Walker, 1849)), which was found inside an adult June beetle, *Phyllophaga inversa* (Horn, 1887). The association of this species with *Solenopsis* sp. was reported by Masner and García (2002), but without indication of the date or location of the observation.

Distribution. Recorded only from the USA.

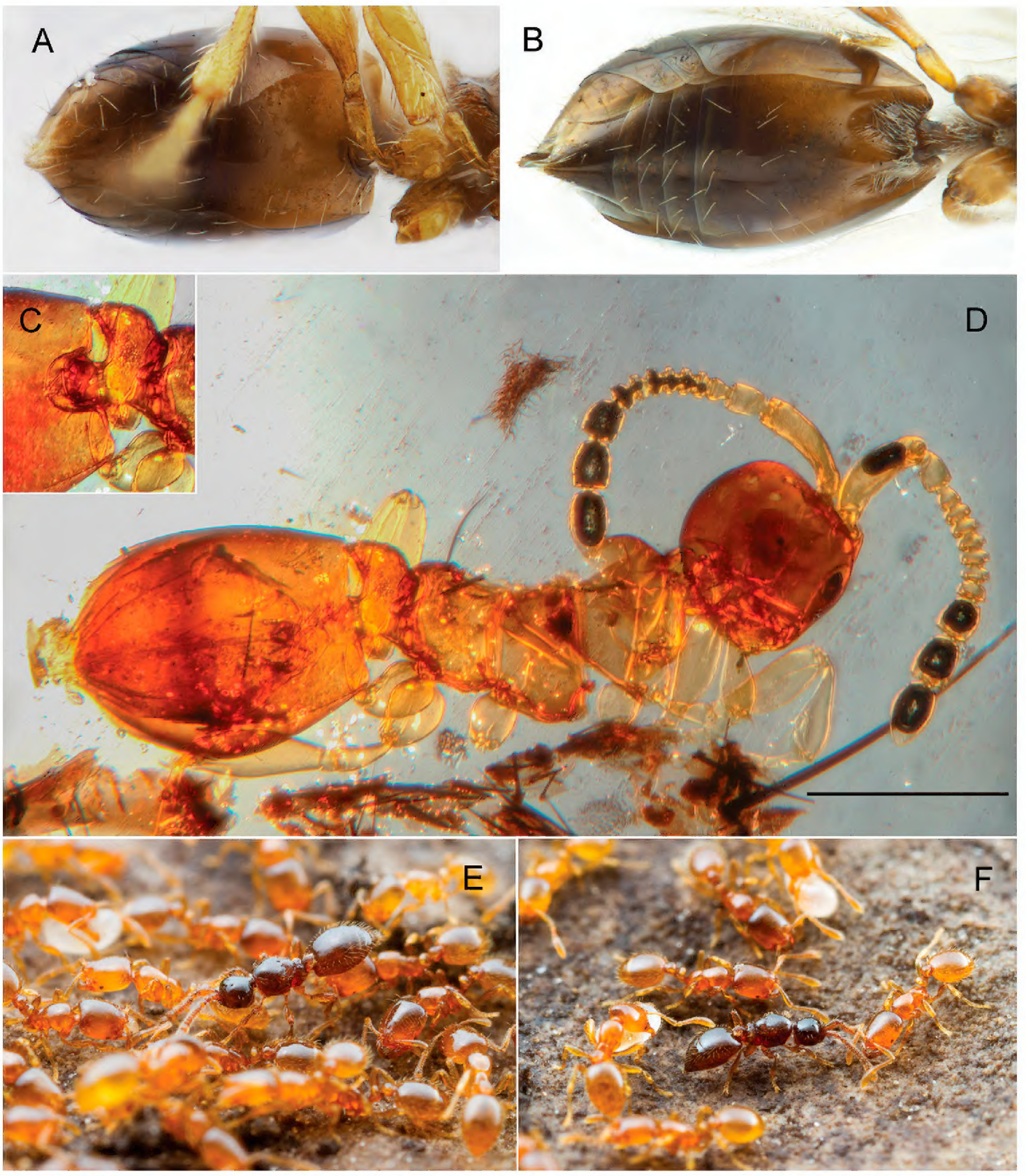

Figure 1. *Bruesopria americana* (**A**), *Lepidopria masneri* (**B**), *B. aberrans*, comb. nov., female, slide of holotype (**C, D**) and *Bruesopria* sp.(**E, F**): **A, B** metasoma, ventral view **C** base of metasoma **D** habitus, dorsolateral view **E, F** female of *Bruesopria* sp. in the colony of thief ant *Solenopsis molesta* (Say), image Alex Wild, used by permission.

Remarks. Masner and Muesebeck (1968) reported on the type of *Lepidopria aberrans* Brues and reported that this species was doubtfully placed in this genus. Later, Huggert and Masner (1983) additionally noted that it may belong to the Nearctic genus *Bruesopria* Wing. This species was not mentioned again until 2002, when Masner and García wrote about it as a member of the genus *Bruesopria*, despite that no new combination had been suggested or justified. However, re-examination of the type spec-

imen of this species and some other available *Bruesopria* specimens, as well as all known *Lepidopria* species, led us to the same conclusion: *Lepidopria aberrans* Brues should be considered a member of the genus *Bruesopria*, as it shares all the characters typical for *Bruesopria* species, as outlined in the comparative diagnosis of this genus above.

Genus *Lepidopria* Kieffer, 1911

Type species. *Lepidopria pedestris* Kieffer, by monotypy.

Genus diagnosis. Small sized insects (1.0–1.8 mm) with yellowish to almost black body, covered with short, erect, evenly distributed setae (usually females more pale and more densely setose than males). Head subglobular in dorsal and lateral views, subtriangular to globular in frontal view; eyes of female small, its largest diameter shorter than length of malar space; palpal formula 4–2. Male antenna 14-merous with only A4 to A3–A4 modified; female antennae 12-merous, with more or less abrupt 4-merous clava to clava indistinct; A1 about as long as four following antennomeres combined; A4–A8 from subquadrate to transverse. Propleuron, mesopleuron ventrally, metapleuron, lateral side of propodeum and petiole covered with dense setation or foamy structures; mesoscutum transverse, without notauli, almost flat but slightly convex antero-medially and depressed postero-medially; mesoscutellum usually with single transverse anterior scutellar pit or it subdivided into two pits; propodeum with more or less distinct median carina that is not elevated anteriorly or carina absent; plica and posterior plical process slightly to moderately projecting. Alate, fore wing as long as body or slightly shorter, with single costal vein developed in its basal third. All legs with cylindrical tarsi, tarsomeres about as long as wide. Petiole in lateral view humped dorsally, elevated above level of base of T2 and not broadened posteriorly; base of T2 distinctly wider than petiole, smooth and flat; base of S2 densely setose, with two groove-like invaginations laterally and median convexity between them; anterior margin of S2 without deep excavation; gaster depressed and ovoid.

Lepidopria bicarinata sp. nov.

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Figs 2, 3

Type material. ***Holotype***, • female: South Korea, Jeju-do (JJ), Jeju-si, Sanduk-ro, 593-40, near Temple Gwaneum rest area (Livestock Research Institute), MT, 1–24.IX.2022, Deokseo Ku & Jeongjun Ahn legs (NIBR). Paratypes: same locality as holotype, 1–16.VII.2022, 16–31.VII.2022, 1♀ and 2♂ (ZISP).

Etymology. The name derives from Latin "bi-" and "carina" and refers to the well-developed two carinae on male A3 and A4.

Diagnosis. Head globular in frontal view (Fig. 2E); female antennae stout, with A9–A11 transverse, A9 about as long as, and as wide as A10 (Fig. 2F); male A3 with carina and without emargination, male A4 slightly enlarged, slightly longer and slightly

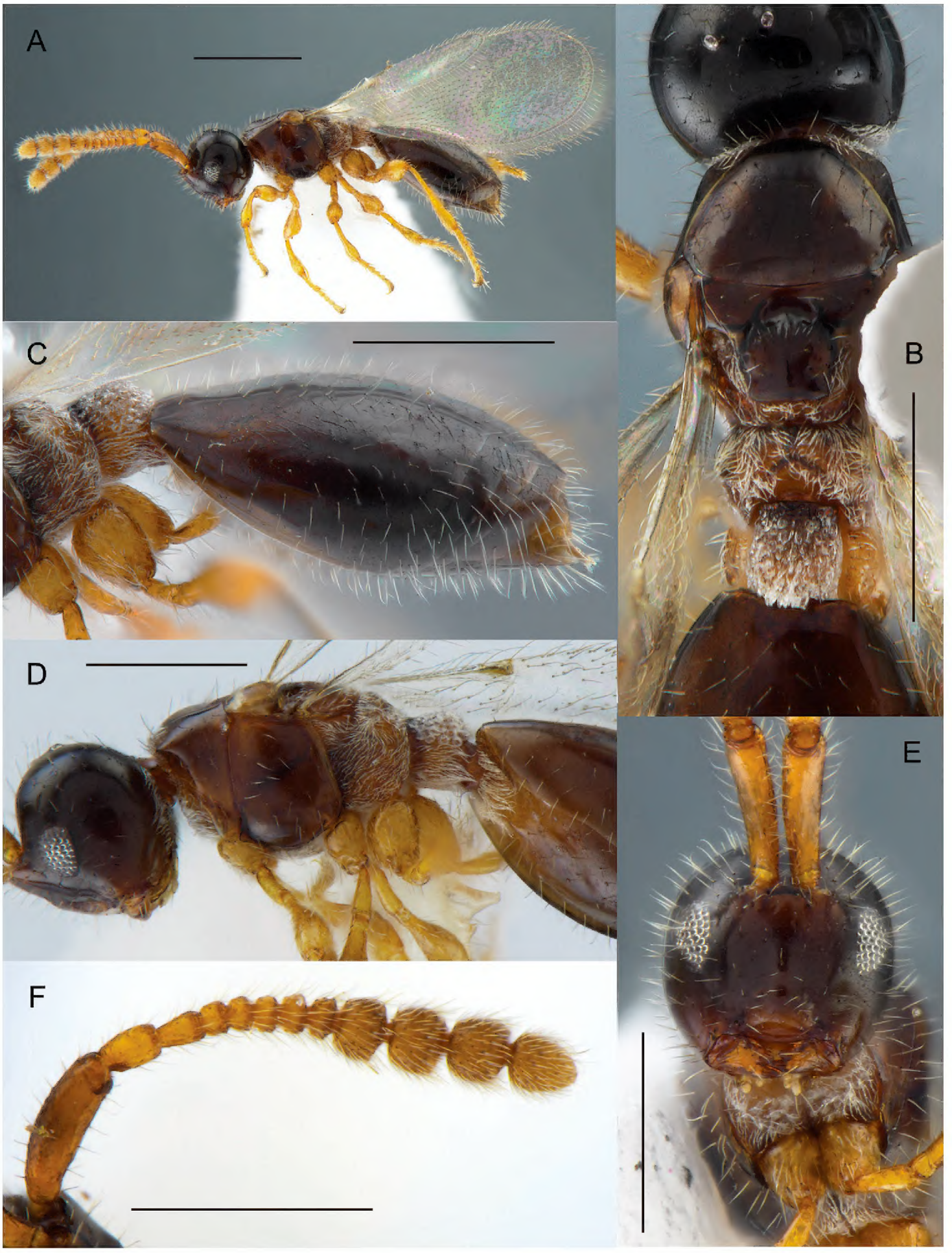

Figure 2. *Lepidopria bicarinata* sp. nov., female. **A** habitus, lateral view **B** head, mesosoma and base of metasoma, dorsal view **C** metasoma, lateral view **D** head and mesosoma, lateral view **E** face **F** antenna, lateral view. Scale bars: 0.5 mm (**A**); 0.3 mm (**B–E**).

wider than A3, with shallow emargination and membranous, pale carina (Fig. 3D, E); mesoscutellum with single transverse scutellar pit (Figs 2B, 3B); propodeum densely setose dorsally, with median carina; plica hardly indicated under setae (Figs 2B, D,

3B); petiole weakly swollen dorsally and projecting upwards, dorsally covered with foamy structure in female and long pale setae in male (Figs 2B, D, 3B).

Description. Female, holotype. Body length 1.5 mm, antennae length 0.85 mm; fore wing length 1.4 mm. Body dark brown except petiole and apex of metasoma brown; tegulae, antenna and legs brownish yellow.

Head rounded, smooth, in dorsal view as long as wide, and 1.15 times as high as long in lateral view, covered with short, erect setae; postgenal cushion dense; ocelli small, inconspicuous, arranged in an almost equilateral triangle; LOL 2.5 times as long as diameter of frontal oculus; OOL large, 3 times as long as POL; compound eye small with fewer than 50 ommatidia; face smooth, epistomal sulcus indistinct; malar space large, 1.1 times as long as height of eye; tentorial pit small and distinct; malar distance about as long as shortest distance between eye in frontal view; mandibles bidentate, with apices slightly overlapping.

Antenna 12-merous, covered with short, semidecumbent to erect setae; A1 slightly compressed and curved, about 3.7 times as long as its greatest width, smooth, shining, and bare ventrolaterally, coriaceous and setose otherwise; in dorsal view A2 cylindrical and 1.8 times as long as wide, in lateral view it tapering towards base; A3 slightly narrower than the A2, 1.5 times as long as wide; A4 and A5 about as wide as A3, subequal to each other and about 1.2 times as wide as long; A6–A8 distinctly transverse and becoming gradually wider; A9–A12 forming abrupt 4-segmented clava, its setation denser and slightly shorter than on other antennomeres; A10 and All subequal, slightly transverse; A9 transverse and slightly wider than A12; A12 ovoid, 1.2 times as long as wide.

Mesosoma about as wide as head; pronotal collar weakly developed (Fig. 2B, D); pronotal shoulders prominent, crossed with sharply projecting pronotal suprahumeral sulcus (Fig. 2D); lateral side of pronotum smooth, with short scattered and erect setation; propleuron with setae and foamy structures on ventral 0.3 and smooth and bare dorsally; mesoscutum weakly convex anteriorly and laterally, and slightly depressed posteromedially, without notauli and covered with short, scattered erect setae; mesoscutellum with transverse and reniform anterior scutellar pit, pit smooth and bare inside; mesoscutellar disc with very weak median carina and elongate rugulae anteriorly, covered with several erect setae laterally; mesopleuron smooth, laterally covered with scattered, short, erect setae; mesopleuron ventrally with short recumbent setae and foamy structures anterior to mid-coxa; metanotum entirely setose, sculptured with scattered setigerous punctures; metascutellum short, with low median carina and weakly projecting lateral carina; ventral side of metapleuron with foamy structure; propodeum and metapleuron entirely densely setose, covered with short, adpressed white setae; metapleuron and lateral side of propodeum without visible carinae; in dorsal view posterior margin of propodeum deeply arcuate: propodeum short medially and significantly longer laterally; lateral and median carinae of propodeum almost parallel, narrow and hidden under setation; nuchal area smooth and bare. Legs moderately robust, covered with short, erect setae similar to those of body; fore tibia with apical spine, its length about half of apical width of tibia; all femora with short basal stalk; hind femur 2.3 times as long as its greatest width. Fore wing 0.9 times as long as body, with single costal vein reaching 0.3 of fore wing length.

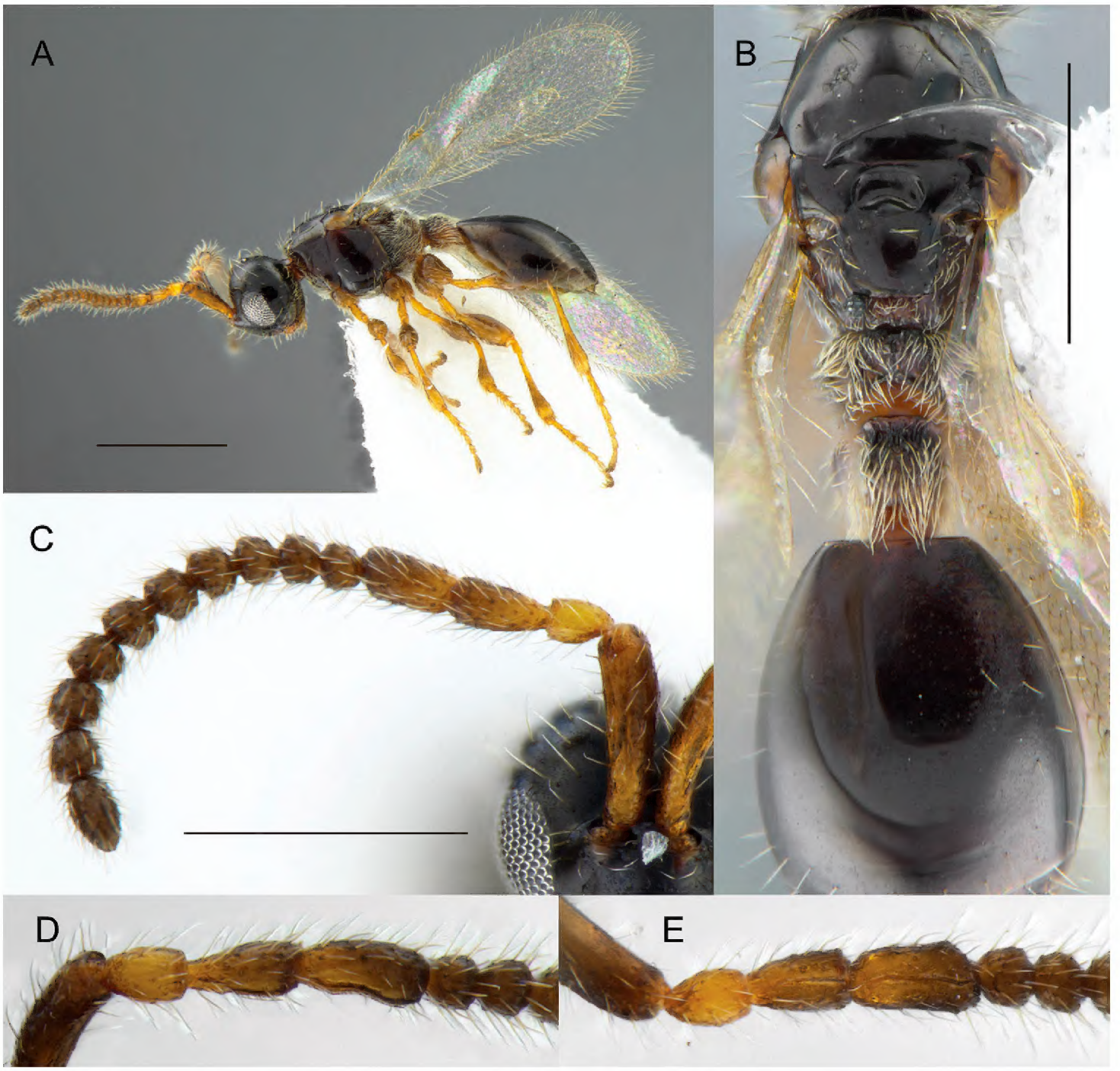

Figure 3. *Lepidopria bicarinata* sp. nov., male. **A** habitus, lateral view **B** mesosoma and metasoma, dorsal view **C** antenna, lateral view **D, E** base of antenna in dorsal (**D**) and lateral (**E**) views. Scale bars: 0.5 mm (**A**); 0.3 mm (**B, C**).

Metasoma. Petiole cylindrical in dorsal view, as wide as long, densely covered with foamy structure on dorsal surface; in lateral view, medial portion slightly swollen upwards; ventral side of petiole covered with short recumbent white setation, not projecting ventrally; gaster about 0.9 times as long as head and mesosoma combined, more than 1.7 times as long as its greatest width, dorsoventrally compressed; T2 dorsally with short, erect, evenly distributed setae, base of T2 flat, wider than petiole; T3–T5 smooth and scarcely setose; base of S2 densely setose, with deep lateral groove and median convexity; basal corners of S2 extending forwards either side of petiole beyond base of large tergite; ovipositor shortly exserted.

Male. Body length 1.4 mm. Differing from female as follows: colour of body black, mandibles and tegula brown, antennae dark brown with A2 yellowish, legs yellowish brown with coxae, femoral and tibial clubs darkened; body less densely setose than in female, especially metasoma, foamy structures developed only on propleuron

ventrally and hidden under long setation; eye and ocelli distinctly larger; malar space short, eye 3.2 times as high as length of malar space; antenna 14-merous, scape as for female, pedicel cylindrical and narrowed at base, 1.5 times as long as wide; A3 and A4 modified, its inner surface curved and with carina, 1.7 and 1.8 times as long as it greatest width respectively; A4 1.2 times as long as A3; A5–A11 about as long as wide; A12 and A13 slightly elongate; A14 ovoid; petiole 1.4 times as long as wide, slightly swollen dorsally and covered with long wight setation; gaster broader, 1.5 times as long as greatest width.

Biology. Unknown.

Distribution. South Korea.

***Lepidopria lloydi* (Ferrière, 1935)**
Fig. 4

Abothropria lloydi Ferrière, 1935: 331, 338.
Lepidopria lloydi: Notton 2014: 42.

Material examined. ***Syntypes*:** • female, "Tanganyika/ Bugambwa/ 7.VI.1933/ J.E.M. Lloyd", "Ex Glossina/ palpalis, pup.", "Abothropria/ lloydi ♀/ Ch. Ferriere Type", "Pres.by/ Imp.Inst.Ent./ B.M. 1935-231", "B.M. TYPE/ HYM./ 9.678", "NHMUK015934128", "♀ SYNTYPE/ *Abothropria/ lloydi*/ Ferrière, 1935/ det. D.Notton, 2009"; male, "Tanganyika/ Bugambwa/ 7.VI.1933/ J.E.M. Lloyd", "Ex Glossina/ palpalis, pup.", "Abothropria/ lloydi ♂/ Ch. Ferriere Cotype", "Pres.by/ Imp. Inst.Ent./ B.M. 1935-231", "NHMUK015934129", "♂ SYNTYPE/ *Abothropria/ lloydi*/ Ferrière, 1935/ det. D.Notton, 2009".

Diagnosis. Small size (1.0–1.5 mm) wasps; female antennae slender with non-abrupt clava (Fig. 4D); male antennae with A3 and A4 modified, both with deep excavation and carina: A3 apically, A4 basically (Fig. 4A, B); male A1 swollen medially; pronotal shoulders not projecting in dorsal and lateral views, without pronotal supra-humeral sulcus, with dense pronotal cushion (Fig. 4A, C–E); mesoscutellum rounded in dorsal view, anterior scutellar pit present as transverse smooth and shallow depression; axillar depression small and shallow, with distinct pit present between it and anterior scutellar pit (Fig. 4A green arrow, C); propodeum very short medially, with low and wide median carina and without plicae, setose dorsal and laterally (Fig. 4C–E); metapleuron bare, with depression posteroventrally near base of hind coxa (Fig. 4E blue arrow); petiole strongly swollen dorsally and projecting upwards, smooth and bare anterodorsally and covered with long pale setae on rest surface (Fig. 4C–E); base of S2 with dense long setation.

Biology. *Lepidopria lloydi* is a parasite of *Glossina palpalis* (Robineau-Desvoidy, 1830) puparia (Ferrière 1935).

Distribution. East Africa (Tanganyika).

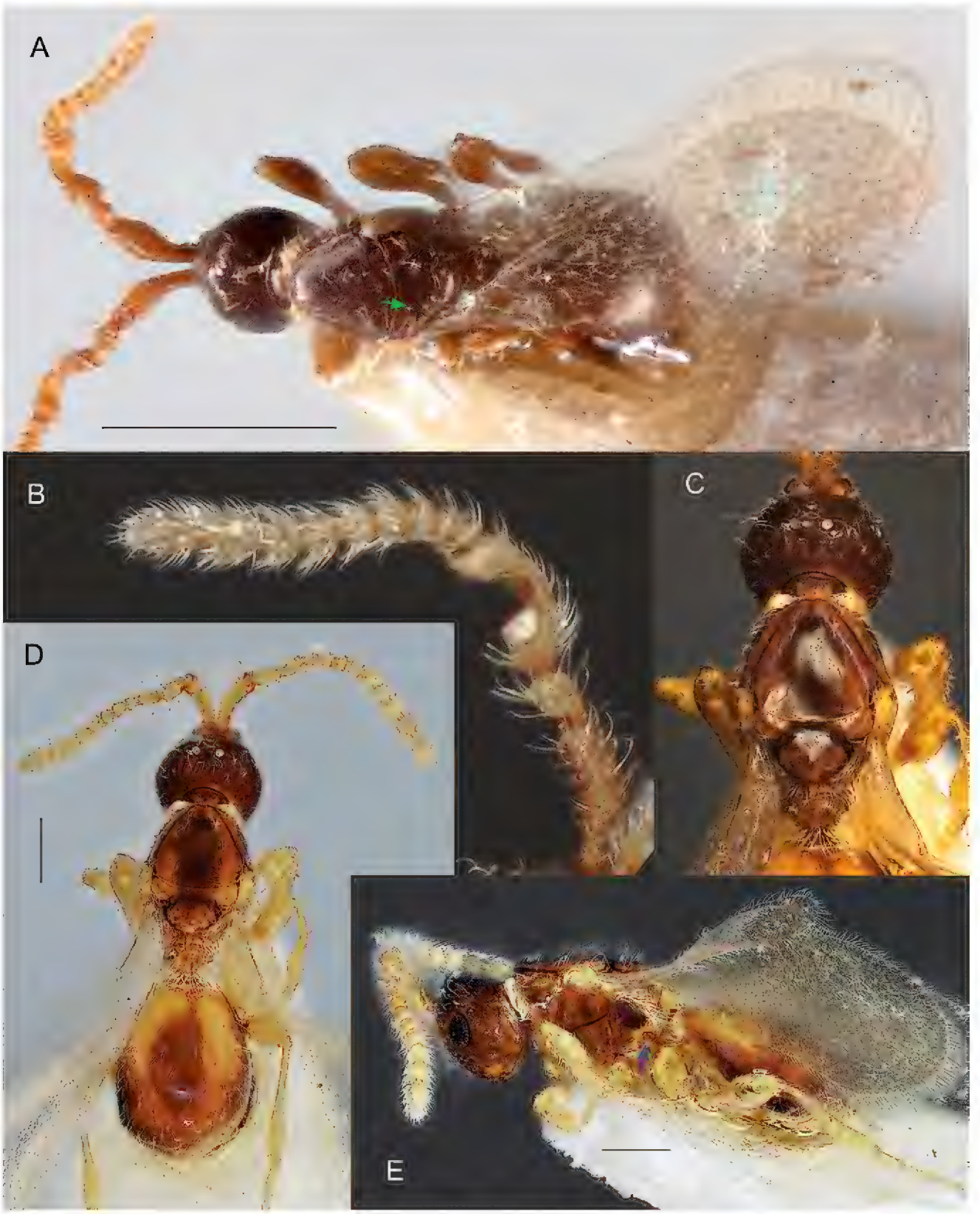

Figure 4. *Lepidopria lloydi*, female (**C, D**) and male (**A, B**) syntypes. **A, D** habitus, dorsal view **B** antenna **C** head and mesosoma, dorsal view **E** habitus, lateral view. Scale bars: 0.5 mm (**A**); 0.2 mm (**D, E**).

Lepidopria masneri Notton, 1994

Figs 5–7

Lepidopria masneri Notton, 1994: 65.

Material examined. • Russia, Primorsky Terr., 10 km SE from Chernigovka, 27.VII.1996, S. Belokobylskij leg., • 1♂ (ZISP). Japan, Honshu, Ibaraki Pref., Tsukuba, 15–25.

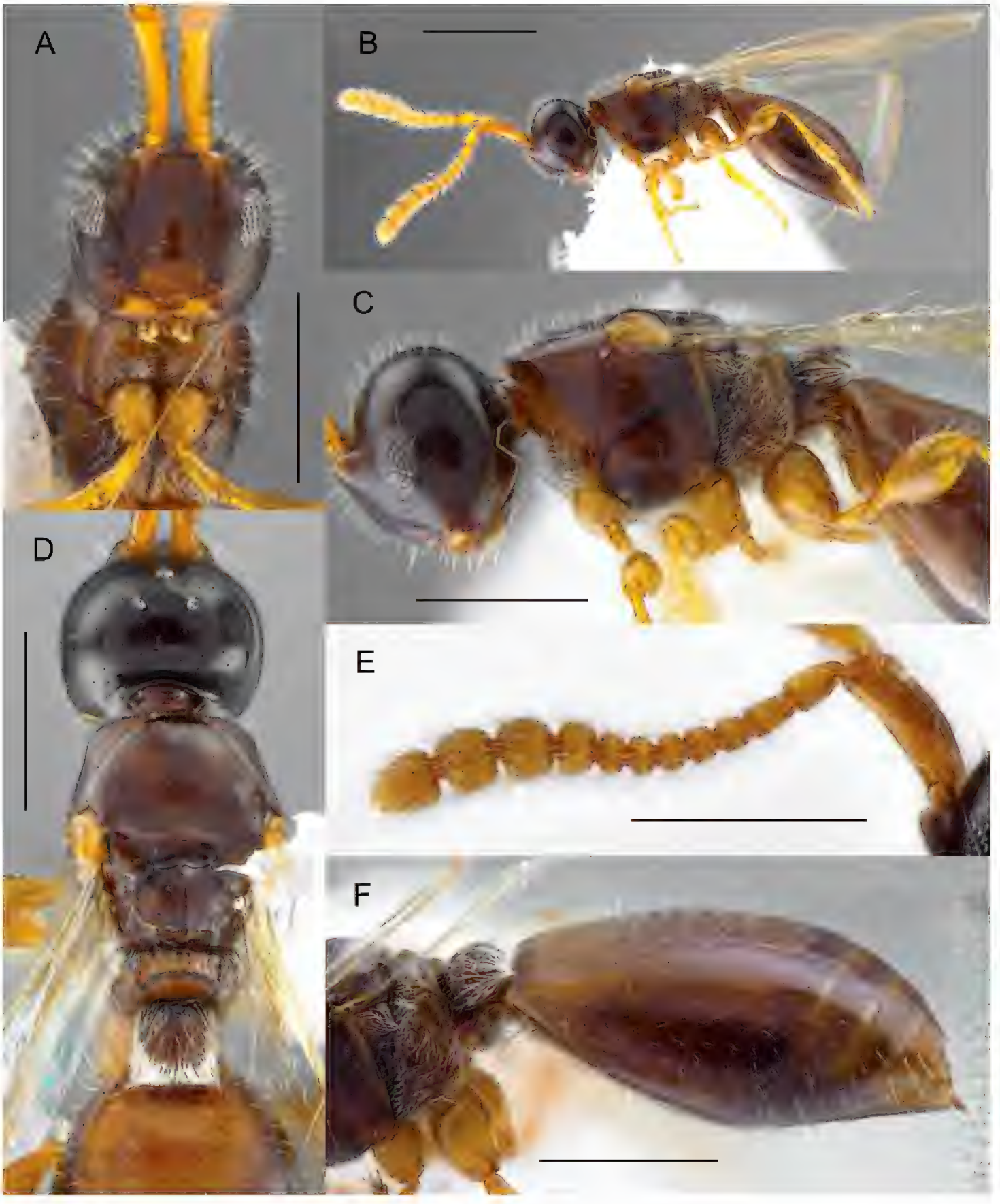

Figure 5. *Lepidopria masneri*, female. **A** face **B** habitus, lateral view **C** head and mesosoma, lateral view **D** head, mesosoma and base of metasoma, dorsal view **E** antenna, lateral view **F** metasoma, lateral view. Scale bars: 0.5 mm (**B**); 0.3 mm (**A, C–F**).

IX.1999, S. Belokobylski leg., • 1♂ (ZISP). South Korea, Gangwon-do, Goseong-gun, 24.VII–07.VIII.2018, MT, Hyung-Keun Lee leg., • 1♂ (SMNE); Jeju-do, Jeju-si, Sanduk-ro, 593-40, near Temple Gwaneum rest area (Livestock Research Institute), MT, 1–16.VII.2022, Deokseo Ku & Jeongjun Ahn legs, • 1♀, 2♂ (SMNE, ZISP); Gyeongsangnam-do, Geochang-gun, Namha-myeon, Yanghang-ri, 36.6752N, 127.5481E, 25

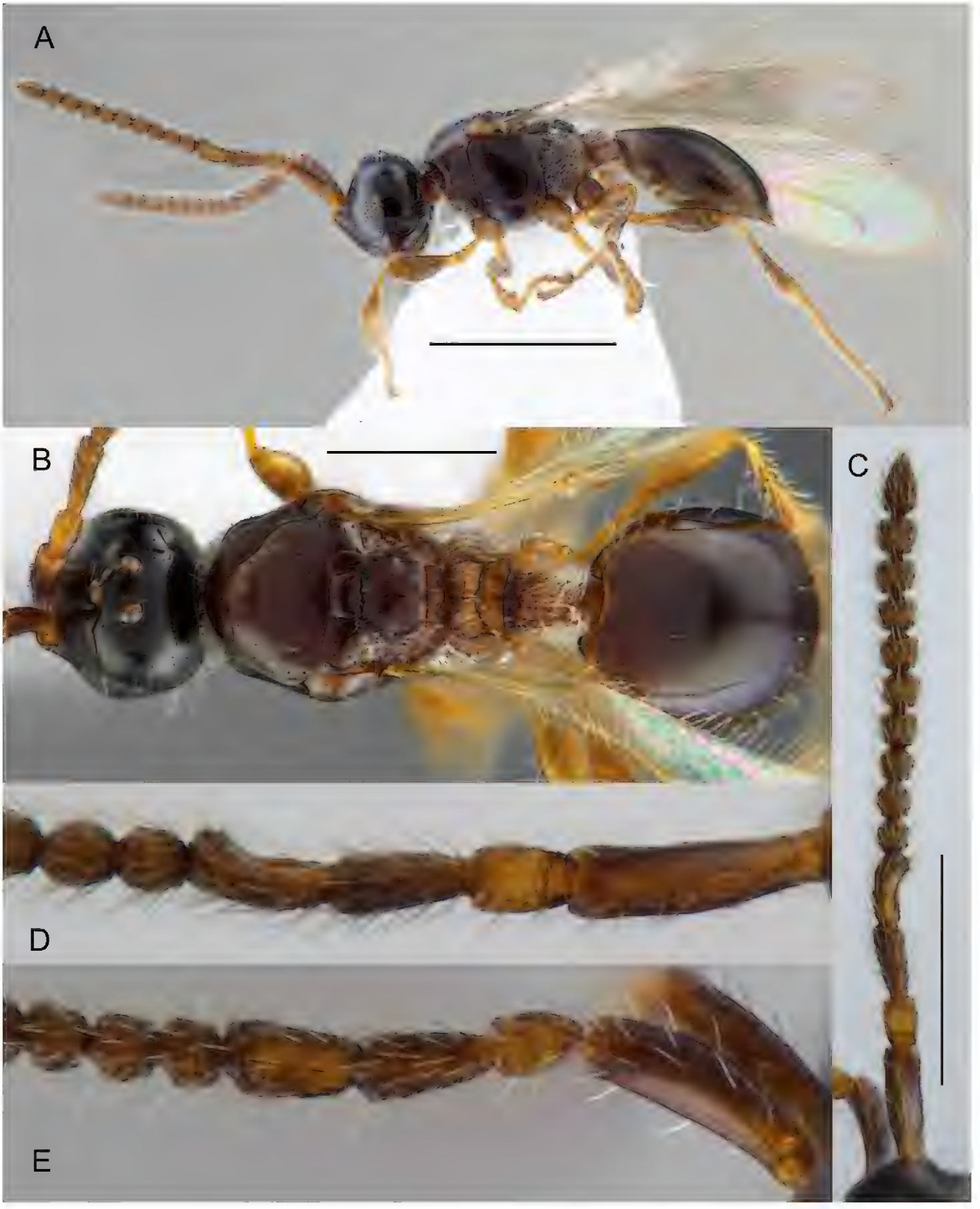

Figure 6. *Lepidopria masneri*, male. **A** habitus in lateral view **B** head, mesosoma and base of metasoma, dorsal view **C** antenna, dorsal view **D, E** base of antenna, dorsal (**D**) and lateral (**E**) views. Scale bars: 0.5 mm (**A**); 0.3 mm (**B, C**).

and 27.VI.2023, E. Tselikh leg., • 1 gynandromorph and 2♂ (ZISP); Busan, Nam-gu, Yongho-dong, Igidae Park, 23.III.2024, Seonwoo Yoon leg., •1♀ (UATC).

Diagnosis. Head globular in frontal view (Fig. 5A); female antennae stout, with A9–A11 transverse, A9 distinctly smaller than A10 (Fig. 5E); male A3 not modified,

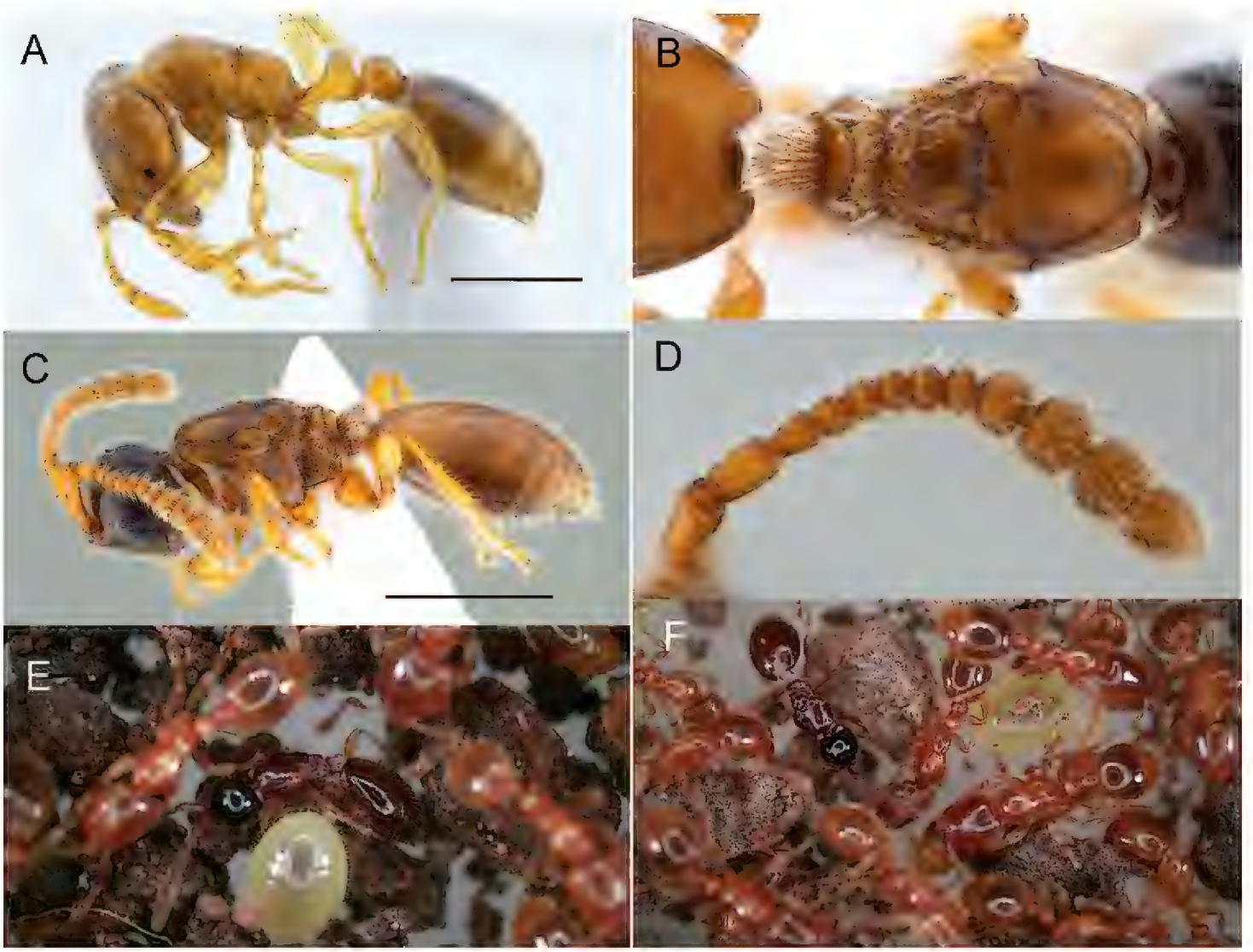

Figure 7. *Lepidopria masneri* (**B–D**) and *Solenopsis japonica* (**A**). **A, C** habitus, lateral view **B** mesosoma and base of metasoma, dorsal view **D** antenna, dorsal view **E, F** female of *L. masneri* in the colony of *S. japonica.* Scale bars: 0.5 mm.

male A3 and A4 subequal in length and wide (Fig. 6D, E); A4 with emargination and membranous pale carina developed from 0.3 and reaching to 0.8 of this segment length (Fig. 6D); mesoscutellum with single transverse scutellar pit (Figs 5D, 6B); propodeum with low and wide median carina and distinct plicae, finely setose dorsally, with few thin scattered setae (Figs 5D, F, 6B); petiole weakly swollen dorsally and projecting upwards; it partly bare to completely covered with beard of long white setae directed backwards (Figs 5D, F, 6B).

Variation. Significant variation was observed in the structural features of the propodeum and petiole (Figs 5, 7): median propodeal carina and transverse carina of the metasomal depression wide and smooth, to narrow and form ridges; dorsal side of propodeum smooth, shining and almost bare to finely setose and coriaceous (Fig. 7B); lateral side of petiole setose to partly covered with white foamy structures (Fig. 7C).

Biology. The dealated female of this species was found in March in a soil chamber near Busan in the Republic of Korea, alongside *Solenopsis japonica* Wheeler, 1928 (Fig. 7). According to our observations, the female of *L. masneri* was clearly integrated into the *S. japonica* colony and roamed freely without being attacked (Fig. 7E, F).

Distribution. *Russian Far East, Japan, South Korea (Notton 1994).

Lepidopria pedestris Kieffer, 1911

Figs 8, 9

Lepidopria pedestris Kieffer, 1911: 870.

Material examined. ***Holotype***, • female, "M. Fasce [mountain in Liguria]/ VIII [18]84/ Ganeva [province of Genoa]", "Lepidopria/ pedestris K.", all other labels are in Fig. 8B. Non-type material: Bosnia and Herzegovina, Stari Most, 29.VI.1959, Hadristevie leg., from tachinid fly developed in *Melolonta melolonta* (Coleoptera, Scarabaeidae).

Diagnosis. Head subtriangular in frontal view (Fig. 9A); female antennae moderately slender, with only A6–A8 subquadrate, all other flagellomeres slightly to distinctly elongate, A9 almost equal to A10 (Fig. 8A); male A3 not modified; male A4 strongly enlarged, distinctly longer and wider than A3, with deep emargination and strong, pigmented carina (Fig. 9A, D); anterior scutellar pit more or less distinct subdivided into two pits (Figs 8A, B, 9A, D); propodeum without median carina, its dorsal side very sparsely setose and finely rugose between plicae (Figs 8A, B, 9B), plica present but hardly indicated; petiole distinctly swollen dorsally and projecting upwards, smooth and bare anterodorsally and otherwise covered with long pale setae (Figs 8A, 9B, E).

Biology. The host of *L. pedestris* is a tachinid fly that develops in *Melolonta melolonta* (Coleoptera: Scarabaeidae) (Huggert and Masner 1983). *Lepidopria pedestris* is symphilic in the nests of the ant *Solenopsis fugax* (Hölldobler 1928; Lachaud 1980, 1981a, b, c, 1982; Lachaud and Passera 1982).

Distribution. South Europe: Italy, France, Germany, *Bosnia and Herzegovina (Kieffer 1911; Höllobler 1928; Lachaud and Passera 1982).

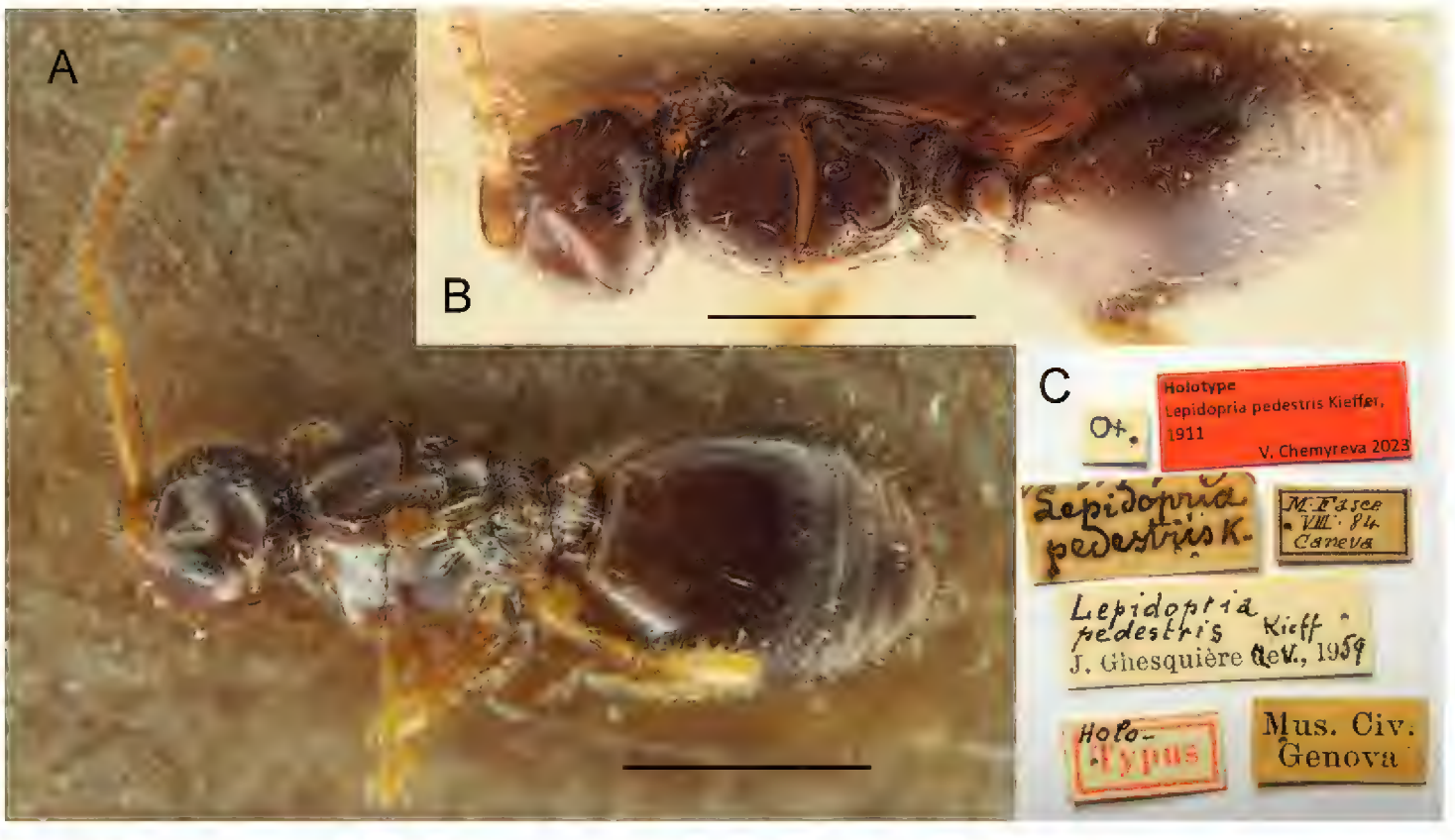

Figure 8. *Lepidopria pedestris*, female, holotype. **A, B** habitus, dorsolateral (**A**) and dorsal (**B**) views **C** labels of the holotype. Scale bars: 0.5 mm.

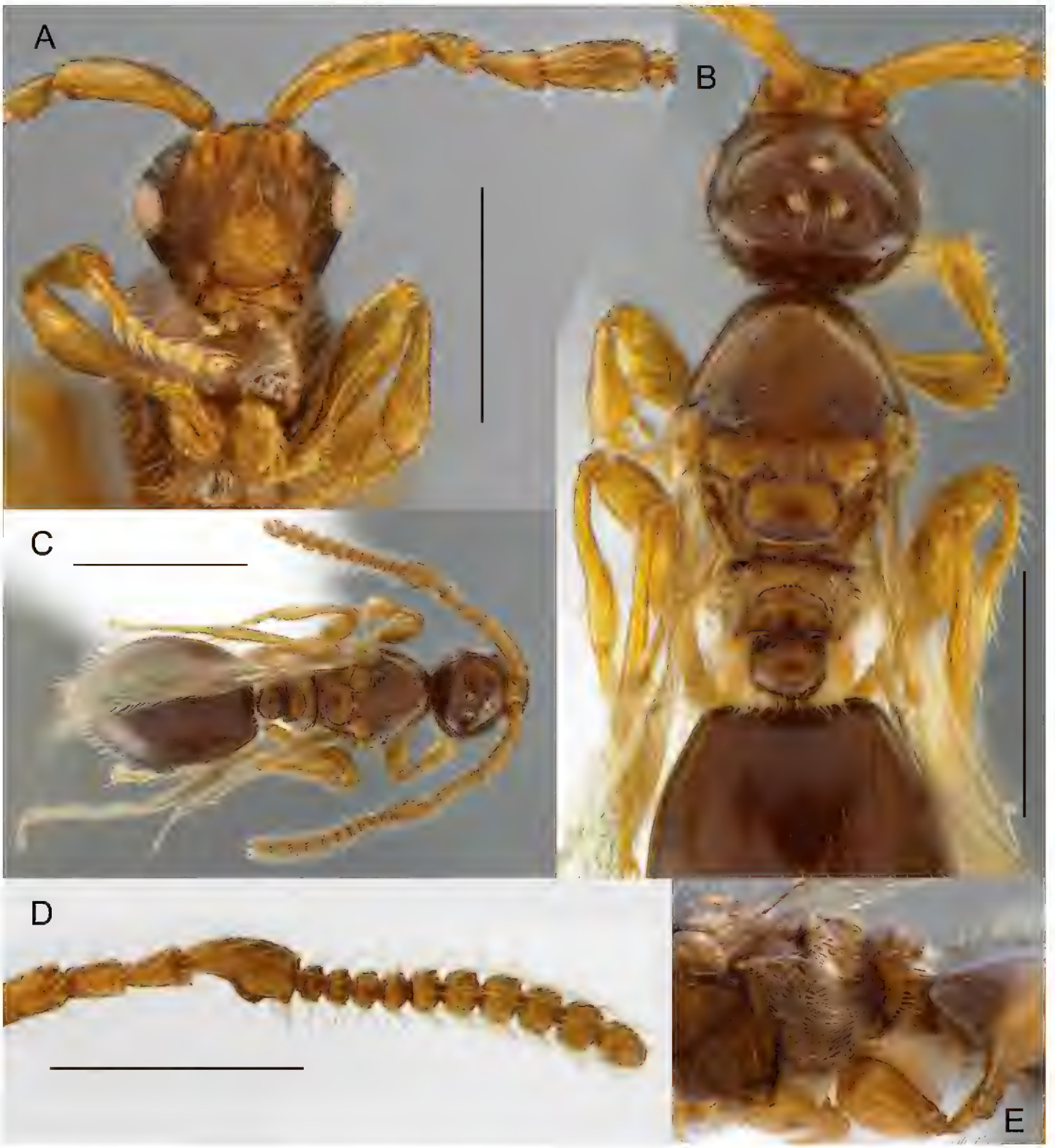

Figure 9. *Lepidopria pedestris*, male. **A** face and base of antennae **B** head, mesosoma and base of metasoma, dorsal view **C** habitus, dorsal view **D** flagellum, dorsal view **E** petiole, lateral view. Scale bars: 0.5 mm (**C**); 0.3 mm (**A, B, D**).

Remarks. Huggert and Masner (1983) reported about "an interesting case of simultaneous parasitism by *Lepidopria pedestris* Kieffer and *Trichopria inquilina* Kieffer on a tachinid puparium in an adult may beetle, *Melolontha melolontha* Linnaeus is known to us from Yugoslavia (specimens in Nat. Museum, Praha)". The male specimen from Bosnia and Herzegovina mentioned above most likely belongs to this group of specimens, and we are providing its label data for the first time here. Dr Jan Macek kindly presented it to us many years ago and it is now stored in ZISP.

Key to the all species of *Lepidopria* Kieffer

1 Female antennae slender with non-abrupt clava (Fig. 4D); male A1 swollen medially, A3 and A4 modified with deep excavation (Fig. 4A, B); pronotum with dense pronotal cushion; borders of anterior scutellar pit indistinct, smoothed (Fig. 4A, C) ..... ***L. lloydi* (Ferrière)**

– Female antennae stout or/and with more or less distinct 4-segmented clava (Figs 1A, 2F, 5E, 8A); male A1 cylindrical, A3 not modified or, at least, without excavation; pronotal cushion reduced (Figs 2D, 5C); borders of anterior scutellar pit distinct (Figs 2B, 3B, 5D, 6B, 9B) **2**

2 Petiole strongly swollen dorsally and projecting upwards (Fig. 9E); pronotal shoulders not projecting in dorsal view, without pronotal suprahumeral sulcus (Figs 8A, 9B); anterior scutellar pit subdivided into two pits, with raised area in the middle (Figs 8A, C, 9B); head subtriangular in frontal view (Figs 8A, C, 9B); female A9–A11 as long as wide (Fig. 8A); male A4 strongly enlarged, distinctly longer and wider than A3, with deep emargination and strong, pigmented carina (Fig. 9A, D)..... ***L. pedestris* Kieffer**

– Petiole weakly swollen dorsally and projecting upwards (Figs 2D, 3A, 5F, 6A); pronotal shoulders distinctly projecting in dorsal view, with sharp pronotal suprahumeral sulcus (Figs 2D, 5C); anterior scutellar pit not subdivided into two pits (Figs 2B, 3B, 5D, 6B); head globular in frontal view (Figs 2E, 5A); female A9–A11 transverse (Figs 2F, 5E); male A4 slightly enlarged, slightly longer and almost not wider than A3, with moderately shallow emargination and membranous, pale carina (Figs 3D, E, 6D, E) **3**

3 Propodeum very finely setose dorsally (Figs 5D, 6B); female petiole partly bare to setose dorsally (Fig. 5D); female antennae with A9 distinctly shorter and narrower than A10 (Fig. 5E); male A3 not modified (Fig. 6D, E) .... ***L. masneri* Notton**

– Propodeum densely setose dorsally (Fig. 2B); female petiole covered with foamy structure dorsally (Fig. 2B); female antennae with A9 about as long as A10 and as wide as A10 (Fig. 2F); male A3 with carina (Fig. 3D, E)..... ..... ***L. bicarinata* sp. nov.**

Discussion

The generic diagnoses of *Lepidopria* given by Kieffer (1911, 1916) were based on a single species, *Lepidopria pedestris*. Subsequently, Huggert and Masner (1983) carried out a comparative analysis of myrmecophilous species of the Holarctic. Although they did not clarify the generic diagnosis, many diagnostic features were illustrated and used in their key. The description of the genus by Huggert and Masner (1983) is not entirely unambiguous. According to the key provided, *L. pedestris* has a propodeum that is "not

excavated posteriorly, ... with distinct median keel", which does not align with the morphology of the holotype (Fig. 8A, B) and Fig. 6 in Huggert and Masner (1983). In our opinion, the latter illustrated a *Lepidopria* sp. with a posteriorly excavated propodeum, whereas the holotype of *L. pedestris* does not have a median carina (keel). However, this discrepancy is not currently significant, as high variation in these two features has been reported in subsequently described species of the genus (Notton 1994; current study).

The genus *Lepidopria* is most closely related to the Nearctic genus *Bruesopria* (the confused classification of *L. aberrans* may confirm this), and to the Palaearctic genus *Solenopsia* (Masner and García 2002). The differences between *Lepidopria* and *Bruesopria* are given in the comparative diagnosis above. Two described species of *Solenopsia* can be distinguished from *Lepidopria* and *Bruesopria* by having 11-merous antenna with a 2-merous clava in the females. They are also characterised by the presence of a distinct median propodeal carina which is slightly elevated anteriorly and forms a tooth-like, subtriangular structure. Other important diagnostic features of *Solenopsia* (most of which are mentioned in the comparative diagnosis given for *Bruesopria* and *Lepidopria* above) are similar to those of species *Lepidopria* or *Bruesopria*. Currently, we believe that it is not possible to reasonably discuss the synonymy of these genera, as additional morphological, molecular, and biological data on these wasps are required. It must be considered that all three genera may have arisen independently through convergent evolution. However, we would like to note that the life cycles of *B. aberrans* and *L. pedestris* most likely are remarkably similar.

Photos taken by Dr Alexander Wild in Kansas (Fig. 1E, F) confirm once again the connection between *Bruesopria* species and the ant *Solenopsis molesta*. The *Bruesopria* in these photos either belongs to the *B. aberrans* species, as it has 12-merous antennae (two other described species of this genus have 11-merous antennae) and 3-segmented clava with slightly elongated segments that are nearly equal in width and about twice as wide as A4–A8 (clavameres are transverse and much wider in *B. americana* (Brues, 1936) and *B. seeversi* Wing, 1951), or it belongs to an undescribed species of this genus that is morphologically close to *B. aberrans*. Therefore, it is likely that all currently known species of *Bruesopria* are associated with *S. molesta* (Wing 1951).

Unfortunately, the detailed biology of the other species *Bruesopria*, *Lepidopria* and *Solenopsia* is not well understood, but all species of these three genera, if known, are associated with the genus *Solenopsis* (Brues 1916; Lachaud 1980, 1981b, c, 1982; Lachaud and Passera 1982; Masner and García 2002; current study). At the same time, we can state with great confidence that the actual species diversity of these myrmecophilous wasps is significantly greater than is currently recognized. Thus, it cannot be discounted that additional discoveries will eliminate the tenuous boundaries between these myrmecophilous genera.

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